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Evaluating the invasiveness of *Acacia paradoxa* in South Africa

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Abstract

We present the first detailed survey of a population of *Acacia paradoxa* DC. (syn. *Acacia armata* R.Br.), Kangaroo Thorn, in South Africa. The species is listed under the Conservation of Agricultural Resources Act as a category 1 invasive plant and, until 2008, was being managed as part of Working for Water's general alien clearing operations. *Acacia paradoxa* is currently restricted to a small population (~11,350 plants over ~295 ha) on the northern slopes of Devil's Peak, Table Mountain National Park in the Western Cape. Its distribution is highly clumped, and at a local scale it has formed thick stands of up to 20 plants m^{-2}. Using a bioclimatic model we predict that it has a large potential distribution in South Africa, especially along the southern coast. We confirmed the categorisation of *A. paradoxa* as a potential landscape transformer that requires immediate control by conducting a formal risk assessment using the Australian Weed Risk Assessment system. However, the population appears to be spreading slowly, and, while there is a significant seed-bank in some places (~1000 seeds m^{-2}), this is largely restricted to below the canopy of existing plants. Therefore, the population has not and likely will not rapidly spread in area, and so containment is feasible. Dedicated and thorough annual follow ups are required because plants can produce seeds when they are 1 year old and standard clearing operations have missed flowering plants.

Keywords: Biological invasions; Early detection; Emerging invader; Invasive alien plants

1. Introduction

Australian *Acacia* species were introduced to South Africa during the 19th and 20th centuries for a variety of reasons (Shaughnessy, 1980; Henderson, 2006). Many of these species have become highly invasive, to the extent that some are among the most widespread invasive plant species in South Africa (Wilson et al., 2007). However, there are several Australian acacias that have been introduced to South Africa that have either not established or have only formed small populations (Shaughnessy, 1980).

The costs of controlling invasive species scales exponentially with the size of area infested (Rejmánek and Pitcairn, 2002). Therefore, when a potentially invasive population is identified, it should be assessed as quickly as possible to determine whether control is required or eradication is desirable (McNeely et al., 2001; Wittenberg and Cock, 2001; Simberloff, 2009). In particular, the biology of the species, the suitability of the new environment, and the population dynamics of naturalised populations should be used to evaluate the invasiveness of the species (Mgidi et al., 2007) and to inform management. Weed risk assessment protocols (e.g. Pheloung et al., 1999) are useful tools in this regard, as they help to organise and summarise available data (Gordon et al., 2008).

In this paper we provide the first detailed assessment of the population of *Acacia paradoxa* growing in Table Mountain National Park (Fig. 1a). The species is currently classified as an emerging invader in South Africa (Nel et al., 2004) and is a category 1 invader according to the Conservation of Agricultural Resources Act (CARA).

The aims of this study are to 1) map the current population on Table Mountain, and 2) evaluate the potential of *A. paradoxa* to become a major invader in South Africa.

2. Species description

Acacia paradoxa DC. is a leguminous thorny shrub that grows up to 4 m tall, and produces dense clusters of yellow

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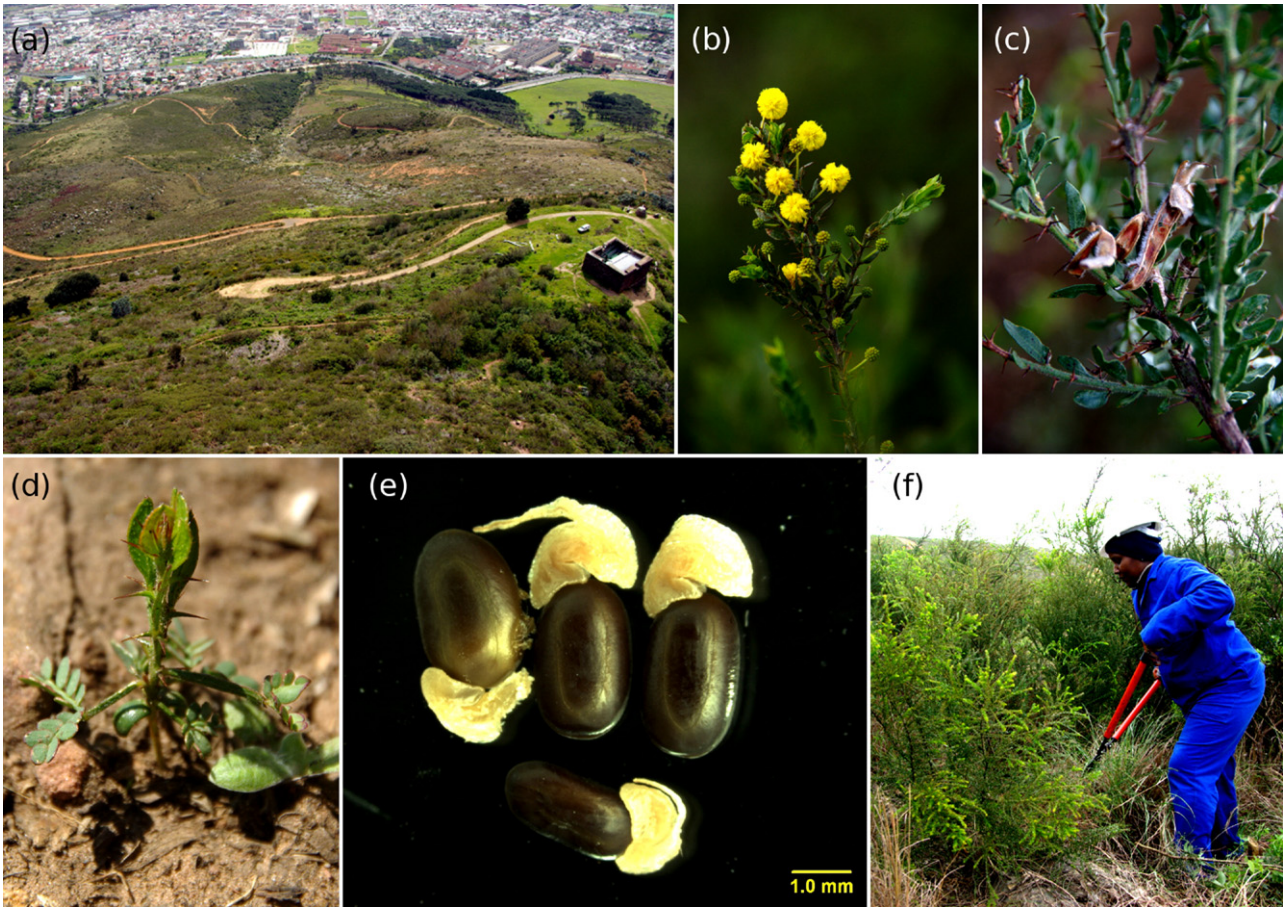


Fig. 1. *Acacia paradoxa* in Table Mountain National Park: (a) A view from above the study site looking down towards Cape Town (the King's Blockhouse and the game park are on the right); (b) flowers and flower buds in September, 2008; (c) old seed pods; (d) 1-month-old seedling; e) fresh seeds with elaiosomes; f) standard management operation, where plants are cut using a saw or brush cutter and herbicide is applied to the cut stems.

flowers (Fig. 1b) during spring (September to November in South Africa). It is native to grassy woodlands and open forests in temperate and sub-tropical regions in Australia (Maslin, 2001; Franco and Morgan, 2007) with annual rainfall ranging from 252 to 1460 mm. Its seeds have small elaiosomes (Fig. 1e) and are formed from November to January in South Africa. In Australia seeds are dispersed by ants, as is the case for many other Australian *Acacia* species (Berg, 1975; O'Dowd and Gill, 1986). There is some debate surrounding its natural distribution, but it is thought to have occurred only in south-eastern Australia prior to European settlement, being introduced to Tasmania and south-western Australia more recently (Franco and Morgan, 2007). The species was commonly planted as a hedge in Australia, but has now been proclaimed a noxious plant in parts of Victoria (Maslin, 2001). It has also been introduced to several countries around the world. In Israel, there is a small naturalised population of *A. paradoxa* close to Jerusalem that probably started as an escape from a tree nursery abandoned in the 1960s, but it is not yet considered invasive (Dufour-Dror and Danin, 2004). In Chile, the species was introduced as an ornamental plant (Macaya, 1999), with no records on whether it has naturalised there. In California, U.S.A., *A. paradoxa* is a declared noxious weed (Calflora, 2008). It is also naturalized in New Zealand (Webb et al., 1988).

The earliest record of *A. paradoxa* we found for South Africa is from a herbarium specimen lodged in the University of Cape Town's Bolus Herbarium dated October 1937. All other herbarium specimens at the Pretoria National Herbarium were collected more recently, and all are from the same part of Table Mountain. This remains the only population recorded in South Africa, despite the fact that it has a distinct morphology and has been included in the main field guide of alien invasive plants for over 8 years (Henderson, 2001). However, systematic management of the population does not appear to have occurred until after 1998, when it was included as part of standard management operations in the area.

3. Materials and methods

3.1. DNA barcoding

To confirm the morphological identification of *A. paradoxa* we used a DNA barcoding approach (Lahaye et al., 2008). Leaf material was frozen in liquid nitrogen and ground by hand prior to DNA extraction. Whole genomic DNA was extracted using a modified cetyltrimethyl ammonium bromide (CTAB) method as described by Doyle and Doyle (1990). The spacer and intron regions of the plastid trnL-F region were amplified using the

universal primers "c" and "f" (Taberlet et al., 1991). PCR consisted of a thermocycle of an initial denaturation of 95 °C for 5 min; 35 cycles at 94 °C for 30 s, 58 °C for 60 s, elongation at 72 °C for 90 s; and final extension at 72 °C for 10 min. Amplified, double-stranded DNA fragments were purified using the QIAquick PCR Purification Kit (Qiagen, USA) and sequenced in both directions using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction kit (PE Applied Biosystems) and an automated sequencer (ABI PRISM 377XL DNA sequencer, PE Applied Biosystems). Sequence data were visualized and edited manually using the Bioedit software version 7.0.8 (Hall, 1999). Using sequence data obtained from GenBank as a reference guide we identified the intergenic spacer between the trnL and trnF. This region is best suited for lower level taxonomic discrimination (Taberlet et al., 1991). To identify similar sequences in GenBank, we used our DNA sequence data in a nucleotide–nucleotide blast search (blastn; Altschul et al., 1997).

3.2. Population monitoring

The study site is situated on the slopes of Devil's Peak in the northern section of the Table Mountain National Park (33.95° S, 18.45° E; Fig. 2a). We started the survey close to the King's Blockhouse where some of the densest stands occur. We sampled all plants in an area of ~4.5 ha between May and August 2008, and measured each plant's height, basal circumference, and took two measurements of canopy diameter (at right-angles); checked each plant for the presence of flower buds, flowers, seed pods, and seeds; and identified whether plants were resprouts. Initially, we removed, bagged, and dried 24 plants of varying sizes for biomass measurements. We took a basal cross-section of the stems in the hope of using age-rings to determine population age structure. All measured plants were either hand-pulled or chopped off at the base followed by spraying the cut stem with herbicide (triclopyr triethylammonium salt–Lumberjack™) as per the Working for Water (WfW) standard clearing protocols.

As the population was much larger than initially expected, it was not possible to measure and cut every plant across the entire area. We subsequently concentrated on mapping all plants so as to obtain a reliable estimate of the total population size and distribution. A systematic survey was conducted based on walking parallel lines (up to 20 m apart; see Cacho et al. (2006) for an evaluation on searching strategies) extending ~50 m beyond the most isolated plant found. The geographic position of each plant found was marked using a hand-held Global Positioning System (GPS Garmin® GPSmap 60CSx, maximum resolution of 3 m), and the tracklogs from the tracking lines recorded in the GPS were used as the basis for drawing a polygon of the surveyed area in Arcview GIS v. 3.2. To improve accuracy, the survey was done primarily while the plants were in flower (August to November). Finally, to check for any plants outside the surveyed area, we scanned the area with binoculars from the top of cliffs above the highest plants recorded.

We used Ripley's L to describe the spatial distribution of occurrence points. Ripley's L averages the number of individuals within a distance (r) of a randomly chosen individual (Perry et al., 2002). We also produced a density map with a Gaussian smoothing kernel using the function density in R (R Development Core Team, 2008). All analyses were done using the surveyed area as the observation window to avoid the assumption that non-surveyed areas contain no plants (Baddeley and Turner, 2005). The presence of plants was visually compared with environmental layers available from South African National Parks (soil type, vegetation cover and number of management operations in the area since 1998).

To estimate the size at reproduction, we regressed the logarithm of plant size against the presence of signs of reproductive maturity (flower buds, flowers, or seed-pods) using a generalised linear model with binomial errors.

3.3. Seed bank and germination

To estimate the size of the seed bank, a corer (auger) was used to sample soil under two different patches of *A. paradoxa*. The first patch chosen contained a couple of very large plants (up to 3 m tall) where old seed pods were present on the plant and in the litter. We set up a grid of 18 m by 18 m that covered the whole canopy and at least 10 m into the neighbouring vegetation. We took a soil core at each 2 m by 2 m intersection, giving a total of 100 soil cores. Each sample was of ~0.0003 m^3 (area section of 33.2 cm^2 by ~10 cm deep). Samples were stored, dried, and sieved using a soil sieve, and the number of *A. paradoxa* seeds were counted. A second area surrounding a relatively isolated plant in open fynbos with a 10 m by 10 m grid, was assessed in the same manner.

From August onwards, we noted extensive germination from the seed-bank, and recorded the number and timing of seedlings emerging under two large plants (each with a canopy area of ~10 m^2). Germination is easy to distinguish from resprouting or regrowth, as the first one or two phylodes of a seedling are bipinnate (Fig. 1d). In general, whenever we observed a plant with bipinnate phylodes, we assumed it was less than 1 year old.

3.4. Management operation

We evaluated the population structure at three different sites that had been cleared at different times prior to our survey (3 weeks, 1 year, and 3 years). At each site we surveyed, measured, and eradicated all plants (using the method previously described).

3.5. Bioclimatic modelling

We used the algorithm Maxent to estimate the realised climate niche of *A. paradoxa* in Australia and, by projection, the likely potential range of *A. paradoxa* in South Africa (Phillips et al., 2006). The bioclimatic variables used to generate the model were part of the WORLDCLIM dataset of global climate layers on a 30 arcsec resolution grid (Hijmans et al., 2005). The bioclimatic variables used in the analysis were the eight most uncorrelated ones according to Loiselle et al. (2008): mean annual temperature, mean diurnal range in temperature, isothermality, temperature seasonality, mean annual precipitation, precipitation of the driest month, precipitation seasonality, and precipitation of the warmest quarter.

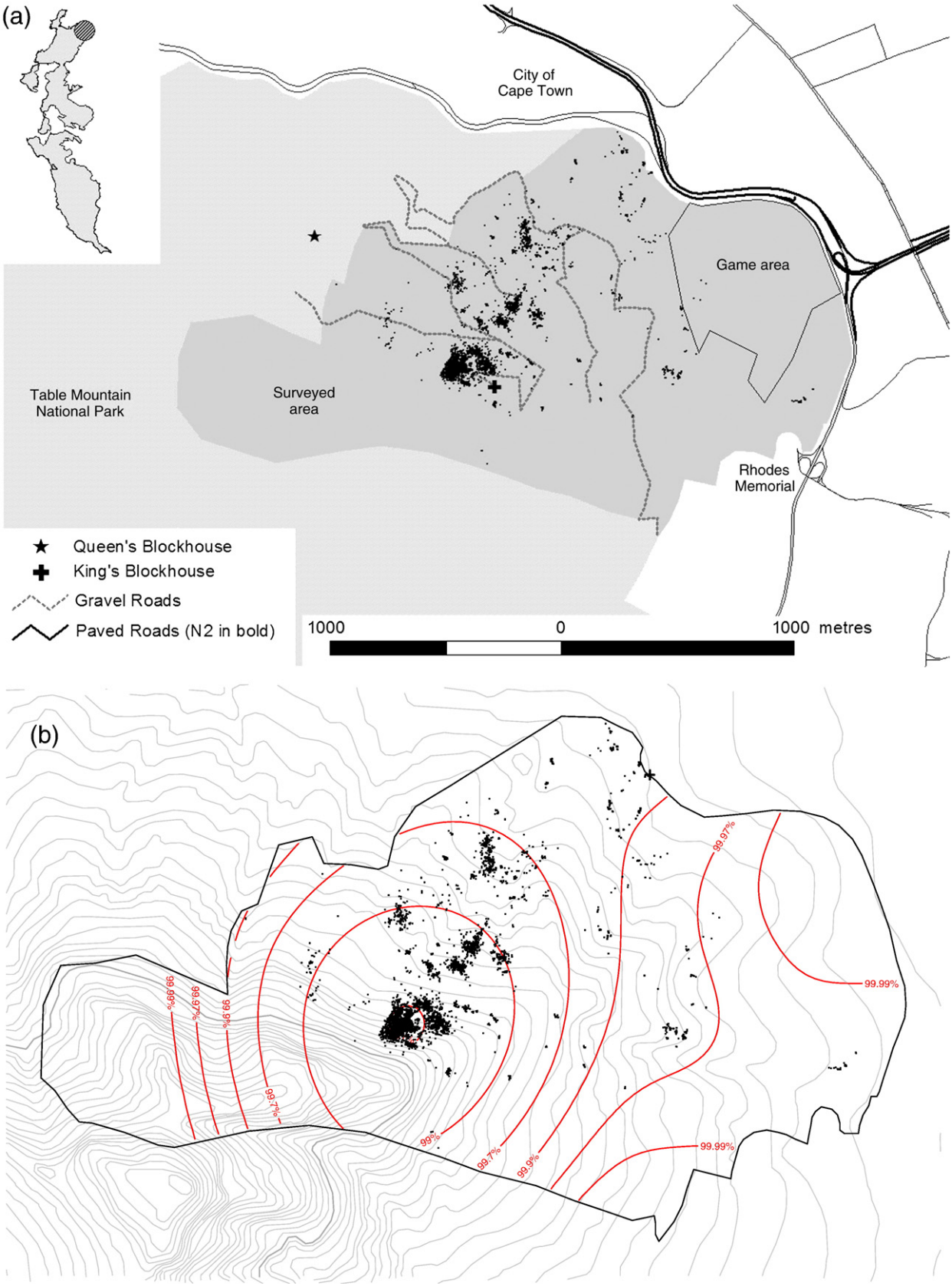


Fig. 2. The distribution of *Acacia paradoxa* on the northern slopes of Devil's Peak, Table Mountain National Park: (a) The surveyed area and major features of this part of the park. The inset in the top-left shows the location of the study site in relation to the rest of Table Mountain National Park. (b) The distribution of plants surveyed, including altitudinal contour lines and the results of an analysis of the density with contours showing the percentage of the population predicted to be in a given area. The upper altitudinal limit of 540 m is shown as a thicker line.

Distribution data in Australia were obtained from georeferenced plant voucher records within the Australian Virtual Herbarium database (http://www.anbg.gov.au/avh/), downloaded on 31 July 2008. The records include occurrences inside and outside the presumed natural range of the species (south-east and south-west Australia). This resulted in a single presence-only dataset for Australia that included all known occurrences.

The model was run using a subset of 100 random points with a minimum distance of 0.5° between records. The minimum distance was required because MAXENT is sensitive to the number of records in an area, and there were multiple herbarium records from a couple of locations in South Australia that would otherwise unduly bias the results. By setting a minimal distance of 0.5° we made sure that only one presence would fall inside any climatic variables grid cell. The remaining occurrence data (1004 records) were used to verify the resulting model using three metrics: area under the curve (AUC), sensitivity, and specificity using the package *PresenceAbsence* in *R* (Elith et al., 2006; McPherson and Jetz, 2007; Freeman and Moisen, 2008). The absence data was based on pseudo-absences (1004 random points with a minimum distance of 0.5° from any presence record to avoid overlapping). The resulting model was then projected onto the current South African climate.

3.6. Risk assessment

To assess the potential invasiveness of *A. paradoxa* in South Africa we applied the Australian weed risk assessment protocol developed by Pheloung et al. (1999). Although this weed risk assessment system was developed for Australia and New Zealand, it performs well across a wide range of geographies (Gordon et al., 2008). We used the data and observations collected in this study as well as information available in the literature. In addition, we assessed the criteria for classifying plant species under the South African Conservation of Agricultural Resources Act (Act No 43 of 1983, with amendments on regulations 15 and 16), concerning problem plants.

4. Results

4.1. DNA barcoding

The complete trnL–trnF intergenic spacer region identified for invasive populations of *A. paradoxa* comprised 416 bp. The Blast algorithm located a 417 bp trnL–trnF intergenic spacer sequence (accession number: AF195678) that was 99% similar to our haplotype (accession number: FJ515909). The only discrepancies between these two haplotypes were two single nucleotide indels at positions 367 and 410. The highest match corresponded to the trnL–trnF intergenic spacer sequence of *A. paradoxa* previously described by Murphy et al. (2000).

4.2. Population status and dynamics

We found 11,348 *A. paradoxa* plants in an area of ca. 295 ha (Fig. 2b). The population extended from the small cliffs just above the King's Blockhouse, 540 m above sea level, down to the border of the Table Mountain National Park. The most isolated plant found was 150 m from its nearest neighbour and the average distance between plants was 1 m (median = 0.4 m), indicating that plants are highly aggregated. The most isolated patch of plants was located 450 m from its nearest neighbour. In fact, the majority of plants (ca. 70%) were within a 5 ha area. Ripley's *L*-function produced a uni-modal distribution, due to the extremely high density in the core of the population relative to other areas. The density map (Fig. 2b) highlights several additional points. The upper altitudinal limit is much more sharply defined than expected; plants appear to be distributed down a couple of the valleys; and there appear to be several clusters of plants, but these clusters have low densities relative to the bulk of the population (and are thus not apparent when using Ripley's *L*).

The plants are found in mesic and wet mesotrophic proteoid fynbos, renosterveld grassland, forest, and thicket. There appeared to be no clear link between presence of plants and soil or vegetation type or with management regimes. Plants were found in all conditions present in the surveyed area, and the limit of the population's spatial range did not appear to match a change in edaphic or other factors.

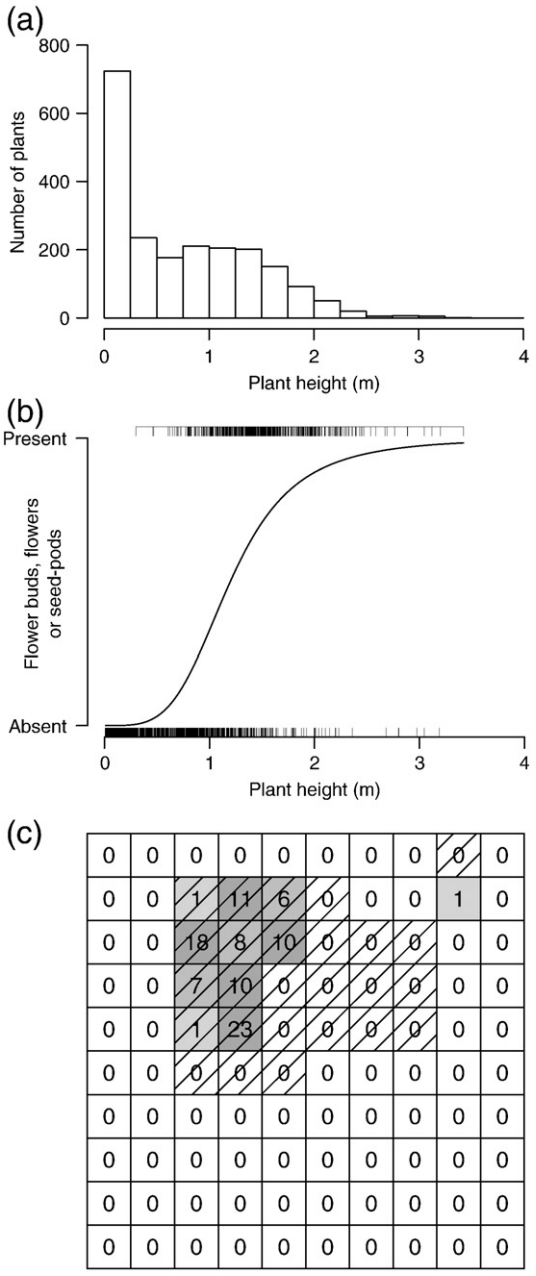
In the study area, *A. paradoxa* plants were up to 3.5 m tall and their canopies covered areas of up to 31.6 m^2. The size distribution of the plants sampled is shown in Fig. 3a. Only 26 plants (about 2%) were found to be resprouts. No growth rings were found when cross sections of stems were sanded and studied under a microscope. The above-ground biomass was found to be best predicted by the basal circumference rather than plant height, canopy volume (estimated as a cone), or canopy area (r^2 of 0.58 vs. 0.08, 0.44, and 0.47 respectively).

Flowering started towards the end of July and continued until mid November. The production of seed pods started towards the end of November. Seedlings were first observed in August, with germination tailing off towards the end of November. Since most survey work was done prior to seed set, we assumed that the presence of flowers or flower-buds was indicative of reproductive maturity. The minimum size of plants at reproduction was therefore 0.3 m, with the majority of plants over 1.5 m producing buds (Fig. 3b).

4.3. Seed banks and germination

We found a total of 95 seeds underneath the canopy of the plants measured for seed banks, with only one seed found outside the canopy (in this case <2 m from the canopy). This suggests a seed bank of approximately 1000 seeds m^{-2} under large plants (3 m tall), but <10 seeds m^{-2} outside the canopy. In the isolated plant (2.5 m tall), only one seed was present in the sample cores, under the canopy, despite the presence of several seed pods.

Within 16 weeks of observing seedlings germinating under two large plants that were cut down we found 82 and 58 seedlings respectively. More than 92% of these seedlings had emerged within 8 weeks after the plants were removed. However, the removal of the trees did coincide with our first observations of germination at undisturbed sites, so we



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0	0	18	8	10	0	0	0	0	0
0	0	7	10	0	0	0	0	0	0
0	0	1	23	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0

Fig. 3. Details of the population at the site: (a) Size distribution of the surveyed population (seedlings and mature plants); (b) The relationship between plant height and reproductive maturity. The presence of flower buds, flowers, or seed-pods was used as a surrogate for reproductive maturity. The line shown is from a fitted generalised linear model with binomial errors and log (plant height) as an explanatory variable; (c) The distribution of seeds in the seed-bank on a 2-m grid. Numbers indicate the number of seeds found in a 33 cm^3 soil sample. The slashed lines indicate the canopy of *A. paradoxa*.

could not ascribe the germination to the removal of the trees *per se*.

4.4. Management operation

The standard management operation for clearing alien plants is usually carried out by a team of ten people, with the instruction to systematically cover the target area and cut down or hand pull all invasive alien plants located (Fig. 1f). The cut stumps are treated with an appropriate herbicide containing blue dye. At the Devil's Peak site, the WfW clearing team is targeting around 15 different species, including *Acacia*, *Eucalyptus* and *Pinus* species.

Within 3 to 4 days after treatment, the leaves of plants were found to have shrivelled and browned. It was therefore easy to spot individuals that had been missed by the control team after clearing.

On the area evaluated 3 weeks after the management operation, ~2.5 ha, the WfW clearing team took 3 h to cover the area in July, 2008. On our return survey we found 153 plants left uncut. Just over half of the missed plants were shorter than 0.5 m (51%), but plants taller than 1.5 m (1% of the total) were also missed including some that were flowering (Fig. 4a). In

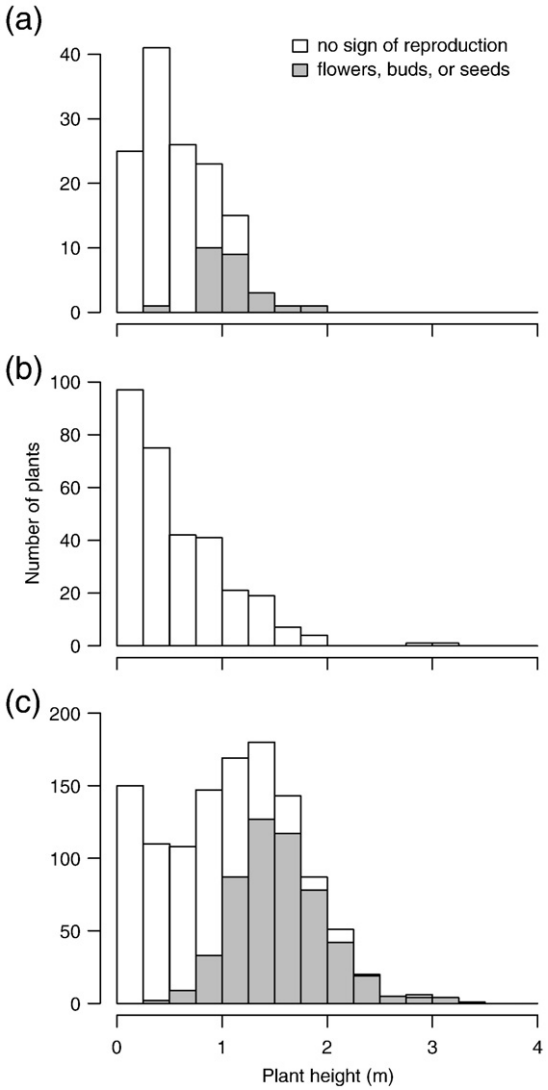

Fig. 4. Size structure of *Acacia paradoxa* individuals greater than 1 year old at three sites: (a) 3 weeks after the last clearing (surveyed in September 2008); (b) 1 year after the last clearing (surveyed in November 2008); (c) 3 years after the last clearing (surveyed between May and August 2008). Individuals younger than 1 year (as shown by the presence of cotelydons) are not drawn because this simply reflects the survey date. That there was no sign of reproduction in the area surveyed 1 year after clearing is probably due to the timing of the survey (after flowering, but before seed-set).

total, 29 reproductively mature plants were left uncut. The return survey included cutting and measuring and took two people 7 h to complete (i.e. 14 field h). It should be noted that the second survey focussed exclusively on *A. paradoxa* and followed the systematic survey described in the methods.

In the area evaluated 1 year after the management operation (November 2008), we found 770 plants in 5.1 ha. None of the plants were flowering, setting flower buds, or had seed pods (Fig. 4b), probably due to the timing of the survey (between flowering and seed-set). Four hundred and seventy two of the plants found had cotyledonal leaves and were relatively small (1–69 cm). The rest (298 plants) ranged from 1 cm (resprout) to 3.05 m tall (Fig. 4b). The return survey included cutting and measuring and took 36 field h to complete.

In the area evaluated 3 years after the management operation (August and September 2008), we found 1181 plants in 4.5 ha. Five hundred and twenty-three plants were setting flower buds or flowers (Fig. 4c). We found densities of up to 20 plants m^{-2}, and the biggest plant of the entire population (3.6 m tall with a canopy area of 31.6 m^2). This area was actually the first area surveyed, and as such we do not have a reliable estimate of how long it would take to complete given the standardised protocol we eventually settled upon.

4.5. Bioclimatic modelling

The bioclimatic model produced a very high accuracy of prediction when projected onto the original distribution data in Australia: AUC = 0.976; sensitivity = 0.965 (sd ± 0.007); specificity = 0.908 (sd ± 0.01). 93.7% of test data were correctly classified (Fig. 5a). The logistic threshold that maximizes the sensitivity and the specificity values is 0.2425. When applying this threshold to South Africa, the existing population of *A. paradoxa* on Table Mountain is found in an area of average predictability (0.2465 and 0.30), and around 13% of the area of South Africa has climatic conditions that are suitable for the growth (and perhaps invasion) of *A. paradoxa*, mainly along the south coast (Fig. 5b).

The bioclimatic variables that contributed most to the results were annual mean temperature (70.6%), and annual precipitation (26.1%). All other variables contributed less then 1%.

4.6. Risk assessment

Using all information found in the literature and the data generated in our study, we could answer 39 out of the 49 weed risk assessment questions, with enough questions answered in each section to complete the analysis (Table 1). The overall score obtained for *A. paradoxa* was 18, comprising 11 points for biogeography reasons, 5 points for undesirable attributes, and 2 points for biology/ecology. As the suggested threshold to consider a species as potentially invasive is 6 (Pheloung et al., 1999), *A. paradoxa* would fail a pre-border evaluation.

In CARA, *A. paradoxa* is listed as a Category 1 invader because its is alien to the country, is already present in South Africa, is invasive in South Africa, is a problem or a potential problem, is not a commercial plantation or subsistence species, is not of ornamental or any other value, and its control is feasible. The recommendation in this case is that it should be immediately contained, indeed it is the species used as an example of this category.

5. Discussion

5.1. The history of Acacia paradoxa in South Africa

From the herbarium records, it is clear that there have been *A. paradoxa* plants on Table Mountain for many decades. Enquiries were made with several land managers and other interested parties in the area, but no records could be found to determine an exact date of or reason for introduction to the country or the study site. There is no mention of this species in reviews of plant introductions to South Africa, or in studies of alien woody plants in the Cape Peninsula (Shaughnessy, 1986; Wells et al., 1986; Richardson et al., 1996). However, we speculate that a few individuals of *A. paradoxa* were introduced close to the King's Blockhouse possibly for hedging or as part of the resident forester's personal interest. The upper altitudinal limit, and largest density of plants recorded are both in the immediate vicinity of the King's Blockhouse (Fig. 2b). Moreover, *A. paradoxa* is commonly used as hedge species in Australia (it is sometimes called hedge wattle), and, while it is available in the nursery trade in Australia, we have no evidence that it was ever traded within South Africa. We also suspect that the introduction may have been part of efforts to afforest parts of Table Mountain that were initiated in 1893 to restore the slopes of Devil's Peak that were suffering erosion (Britton, 2006).

Given that large parts of South Africa are climatically suitable for *A. paradoxa* (Fig. 5), we would also suggest that if plants had been moved around South Africa by humans, either as an ornamental or for hedging, then the species would have naturalised in many more locations (i.e. the isolation of Table Mountain from other areas is the main factor limiting its regional spread).

According to the Park's administration (SANParks) clearing of *A. paradoxa* started in 1998, when it was first identified as a problem species. While some of the areas invaded by *A. paradoxa* have been visited up to five times, others were visited only once (SANParks' Geographic Information System). Some of the areas that were managed more often were also the areas with the highest densities of plants, and according to some of the park rangers these coincide with the areas where the biggest *A. paradoxa* plants were found in 1998.

Therefore, we suspect the current population is the result of a few plants initially introduced as a curiosity, followed by a long history of neglect, then subject, in the past decade, to alien plant clearing operations. While the intention of recent management efforts was to eradicate the population, precise details of what was removed are not available. However, the clearing until now can be categorised as sporadic and partial, focussing mostly on the largest and presumably oldest plants.

5.2. Dispersal

The presence of an elaisome on the seeds (Fig. 1e) suggests that *A. paradoxa* is adapted for dispersal by ants. Native ant

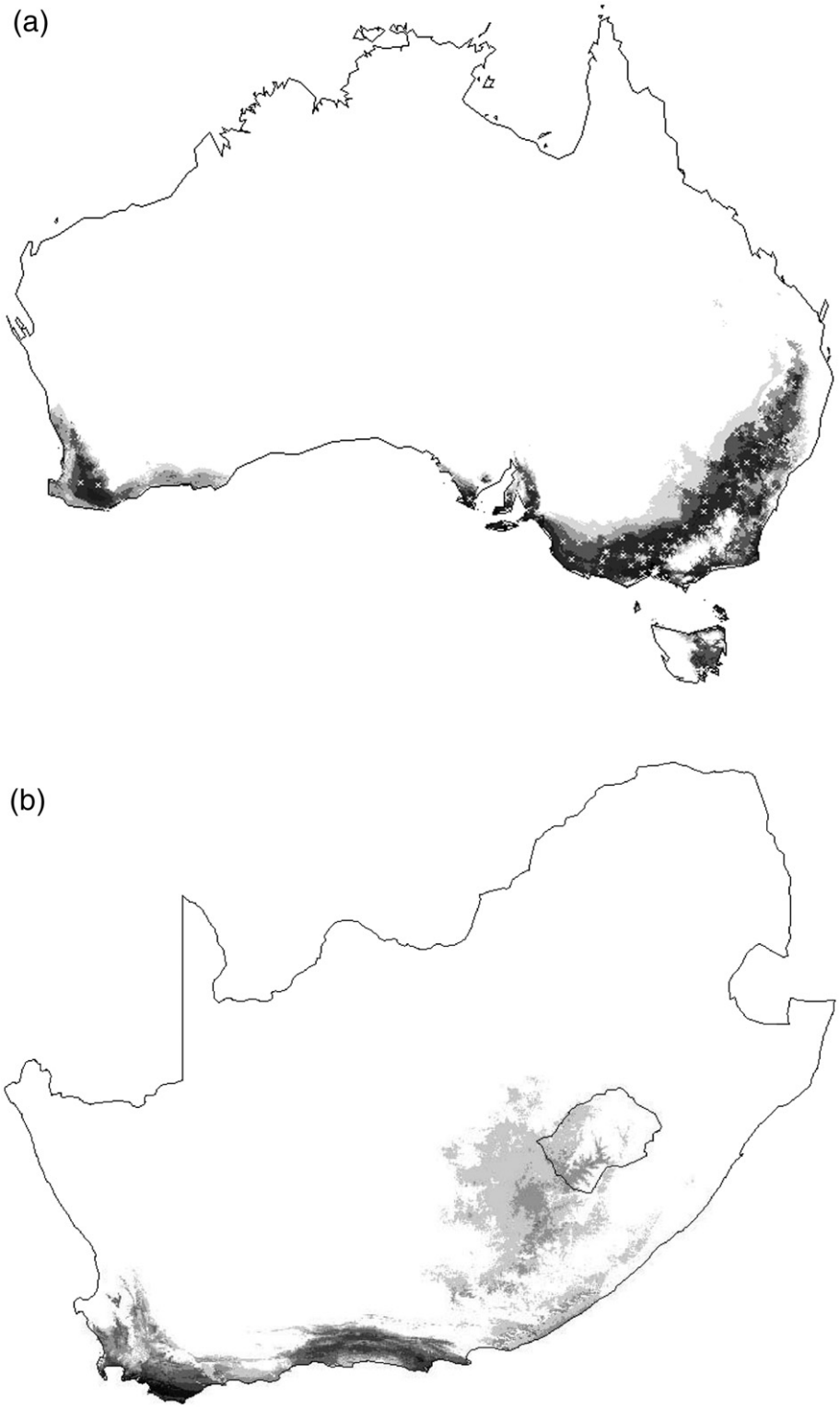

Fig. 5. Predicted climatically suitable potential range for *Acacia paradoxa* in (a) Australia and (b) projected onto South Africa. Suitable areas range from unsuitable (white) to optimal (black). Presence data from herbariums records are shown as (x).

species in the genera *Anoplolepis* and *Pheidole* spp. disperse seeds of *A. cyclops* and *A. saligna* in the Western Cape over short distances (2–3 m) (Holmes, 1990a,b). Moreover, the burial of seeds by ants seems to be important in ensuring escape from rodent predation (Holmes, 1990a), and facilitating the development of dense stands (Holmes, 1990b). While this may be a mechanistic explanation for clumping in *A. paradoxa*, we would argue that if ants are dispersing seeds, there should be a wider distribution of plants given the time scales involved and the population should be spreading up-hill. The sharp upper

Table 1
Risk assessment protocol for *Acacia paradoxa* following the method of Pheloung et al. (1999).

Question	Answer and reason	Ref
Is the species highly domesticated?	No. Used for hedging, but no evidence of strong selection.	1
Species suited to South African climates	High.	Fig. 5
Quality of climate match data.	Intermediate. We relied on herbarium records and a global climatic dataset.	Methods
Broad climate suitability	Yes. Found in sub-tropical, temperate and Mediterranean-type climates.	1, 2
Native or naturalised in regions with extended dry periods (areas with rainfall in the driest quarter less than 25 mm).	No. The species is naturalized only in areas with more than 100 mm of rainfall in the driest quarter.	Fig. 5
Does the species have a history of repeated introductions outside its natural range?	Yes. The species is recorded as introduced in Australia (outside its native range), Chile, Israel, South Africa, New Zealand and the USA.	1, 2, 3, 4, 5, 6
Naturalised beyond native range?	Yes. (as above).	
Garden/amenity/disturbance weed	Yes. The species is naturalised in disturbed areas.	6
Weed of agriculture/horticulture/forestry	No. No records of naturalization in productive areas.	
Environmental weed.	Yes. Species invades natural ecosystems.	
Congeneric weed	Yes.	3, 7, 8
Produces spines, thorns or burrs	Yes. Many thorns!	
Allelopathic	Not known.	
Parasitic	No.	
Unpalatable to grazing animals	Not known.	
Toxic to animals	Not known.	
Host for recognised pests and pathogens	Yes. Cotton cushion scale, *Icerya purchasi*, (Family Margarodidae) were found on plants.	Pers. obs.
Causes allergies or is otherwise toxic to humans	No. No evidence of toxicity or allergies.	Pers. obs.
Creates a fire hazard in natural ecosystems	Not known.	
Is a shade tolerant plant at some stage of its life cycle	Yes. It grows well under large trees and forest.	Pers. obs.
Grows on infertile soils	Yes. The soil of the study area is extremely nutrient poor	Pers. obs.
Climbing or smothering growth habit	No.	
Forms dense thickets	Yes. Up to 20 plants m^{-2}.	Fig. 1, 2
Aquatic	No.	
Grass	No.	
Nitrogen fixing woody plant	Yes. Root nodules noted on some uprooted plants.	Pers. obs.
Geophyte	No.	
Evidence of substantial reproductive failure in native habitat	No. No evidence, but it is partially self-incompatible.	9
Produces viable seed	Yes. Reproduction is by means of seeds only.	10, 11, Fig. 1
Hybridises naturally	Yes. Putative hybrids are recorded between *A. paradoxa* and several other species, especially those in the *A. verniciflua* complex.	1
Self-fertilisation	Yes.	1, 9
Requires specialist pollinators	No. Pollinated by honeybees.	Pers. obs.
Reproduction by vegetative propagation	No. Plants can resprout from cut stems, but there is no evidence of regrowth from fragments.	Pers. obs.
Minimum generative time	Probably 1 year.	Figs. 3, 4
Propagules likely to be dispersed unintentionally	Yes. Road sides are likely pathways.	10
Propagules dispersed intentionally by people	No. Although historically used as a hedge, it is not currently used as an ornamental, or grown privately as far as we know.	Discussion
Propagules likely to disperse as a produce contaminant	No.	1, 2, 11
Propagules adapted to wind dispersal	No. No adaptations present.	
Propagules buoyant	No. No specific adaptation, but likely that seeds float and are suitable for dispersal along rivers.	
Propagules bird dispersed	No. No evidence.	1
Propagules dispersed by other animals (externally)	Yes. Dispersal by ants (in Australia at least).	12
Propagules dispersed by other animals (internally)	No. No evidence.	
Prolific seed production	Possible, but not quantified here. There is a substantial seed bank however.	Results
Evidence that a persistent propagule bank is formed (>1 year)	Yes.	Results
Well controlled by herbicides	Yes. At least on cut stems.	
Tolerates or benefits from mutilation, cultivation or fire	Yes. Resprouts/coppices unless herbicide is applied.	
Effective natural enemies present in the country	No. But some plants were heavily attacked by cotton cushion scale, and disease symptoms were present.	Pers. obs.

[1] Maslin, 2001; [2] Calflora, 2008; [3] Henderson, 2001; [4] Macaya, 1999; [5] Dufour-Dror and Danin, 2004; [6] Randall, 2002; [7] Richardson and Kluge, 2008; [8] Nel et al., 2004; [9] Kenrick and Knox, 1989; [10] Brown et al., 2003; [11] Franco and Morgan, 2007; [12] O'Dowd and Gill, 1986.

altitudinal band, and the general spread down valleys (Fig. 2b) is more consistent with stochastic dispersal through seed drop and gravity, potentially aided by water. This, in combination with occasional short-jump dispersal due to accidental human movement or ants, may be sufficient to explain current patterns of spread.

While birds are a major dispersal agent for *Acacia cyclops* and, to a lesser extent, *A. saligna* (review in Richardson and

Kluge, 2008), the assumed spread rates are inconsistent with rapid local dispersal. We observed signs of seed predation in the field (December 2008) that we speculate were due to feeding by birds. Fresh seeds appeared to have been removed from the seed pods and eaten, but the elaiosome remained untouched. However, we have no evidence that birds disperse viable *A. paradoxa* seeds.

At a regional scale, *Acacia paradoxa* propagules are not likely to be dispersed as product contaminants, are not wind dispersed, and South Africans do not currently cultivate the species. While there is no evidence of effective long-distance dispersal, a new association with a disperser or accidental spread through human influence could quickly change this (Nathan et al., 2008). Regarding the latter point, the proximity of the invasive population to the city of Cape Town and to some important national roads (notably the N2 highway) is particularly worrying (Fig. 2a). Current road-works on the N2 at Hospital Bend are within 100 m of an area where we saw very young *A. paradoxa* seedlings. If *A. paradoxa* seeds became attached to earth-moving equipment, the seeds may potentially be dispersed over long distances. Similarly, we found several large *A. paradoxa* plants, a few of which set seed, growing in the game farm close to the Rhodes' Memorial. If game were moved to a different location, they could potentially spread *A. paradoxa*, but we have not quantified the risk of moving seeds through vehicles or animals.

Given the wide climatic range of climatic conditions under which *Acacia paradoxa* grows in Australia, and the reasonably large potential range predicted for South Africa (see Fig. 5, cf. Nel et al., 2004), we conclude that the range size of *A. paradoxa* is currently restricted on a regional scale due to a lack of long-distance dispersal, in particular a historical lack of human assistance.

5.3. Population dynamics on Table Mountain

The current stage structure is indicative of a young and expanding population. In particular, a large number of seedlings are emerging from the seed bank, leading to a heavily skewed stage-structure. But the population is still restricted to a small area. These observations, of course, do not match with the putative long residence time of the population. While it may simply be the time taken for numbers to build up combined with dispersal limitations, there may be or have been factors keeping the population in a lag phase. *A. paradoxa* is partially self-compatible, mostly needing cross-pollination (Kenrick and Knox, 1989), and so a small initial population may have had limited success. In contrast, plants can reproduce when they are small, certainly after 1 year, and germinable seeds are being produced in significant quantities (e.g. we recorded 5–10 seedlings m^{-2} in some areas).

Alternatively, *Acacia paradoxa* may be a habitat specialist. We could not, however, find an environmental variable correlated with the strong aggregation based on the maps available for the Table Mountain National Park. Plants were observed to grow in a variety of microclimates including exposed erosion slopes, open fynbos, in valleys, and at the fringes of pine plantations. The fact the population is so highly aggregated and has failed to spread more widely on Table Mountain (despite apparently large seed numbers, a wide tolerance of environmental conditions, and its apparent ability to colonise fynbos) suggest that dispersal in this population is indeed highly limited. Similarly slow rates of spread in other introduced populations of *A. paradoxa* in other countries appear to concur with this (Dufour-Dror and Danin, 2004; Calflora, 2008).

We have not directly quantified the impacts of the population of *A. paradoxa*, but by producing dense monoculture thickets, this species might potentially be reducing the frequency and abundance of native plant species at a local scale. Under big plants, native species richness appears much lower than in uninvaded areas; indeed in one thicket the only plants found were *A. paradoxa* and non-native *Solanum* species. *Acacia paradoxa* fixes nitrogen through rhizobial mutualisms (as root nodules are present) and this could have major implications for its invasiveness in the nitrogen-limited fynbos ecosystems. Vitousek and Walker (1989) elegantly showed how nitrogen fixation contributed to the invasiveness and competitiveness of *Morella faya* (Ait.) Wilbur (syn. *Myrica faya* Ait.) in Hawaii, a region similarly limited in soil nutrients, particularly nitrogen. *Morella faya* has altered the soil chemistry by increasing nitrogen up to four fold in invaded areas and this may further facilitate invasion by additional species (Vitousek, 1990). Other Australian *Acacia* species have had similar ecosystem-level impacts in natural fynbos communities in South Africa (Yelenik et al., 2004), and *A. paradoxa* could have comparable impacts if allowed to spread. Substantial alteration of fire behaviour is also likely, as has been demonstrated for other invasive Australian acacias in fynbos ecosystems (Van Wilgen and Richardson, 1985).

5.4. Future management and recent fires

Subsequent to the monitoring reported here, the area has been subjected to dedicated clearing. Using the maps produced in this study, Working for Water teams, under the management of SAN Parks, have started work in the area to systematically clear all large plants. It is the intention of all the stakeholders to repeat such activities on an annual basis, and when the density is low enough, to combine dedicated monitoring with removal.

The area covered by our survey was burnt in an intense wildfire on 16–18 March 2009. While we could previously only speculate on the effect of fire on mature plants, on the seed-bank, and on germination rates, we now have the opportunity to study the impact of fire on the population dynamics and on the potential for management. While plants appear to be able to resprout from cut stems (presumably if the stem is not treated), we saw no evidence of root resprouts, or vegetative reproduction. Given the size of the seed bank, this acacia is clearly more of a reseeder than a resprouter. As such, the impact of fire on the seed-bank will be particularly important in understanding future management.

6. Conclusions and recommendations

Acacia paradoxa grows under a wide range of bioclimatic conditions in Australia, and it is predicted to thrive in several

parts of South Africa, particularly along the southern coast. Under both CARA and the weed risk-assessment protocol (Table 1), *A. paradoxa* is an invasive plant with potential to become a major problem, and legislation should continue to reflect this. However, our study strongly suggests that the invasion is confined to the northern slope of Devil's Peak, Table Mountain National Park, that the population has limited dispersal ability, and that it should be relatively easy to control.

Focussed annual clearing operations (species specific) could reduce, and potentially eradicate, the population. But these operations must be carefully conducted to ensure that reproductive plants are removed and long-distance dispersal is prevented. We recommend an adaptive management approach (Tu et al., 2001) where the outcome of each treatment is monitored and evaluated, so subsequent treatments can be adjusted to be more effective. Further research is needed on the seed bank (persistence, dormancy), and the effect of fire on seed bank dynamics. We are optimistic that, given the development of an appropriate management strategy and sustained political will, *A. paradoxa* will not be present on Table Mountain for another hundred years.

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